

*Evolution of
Feathered Dinosaurs*
Growth and Physiology

*New Perspectives
on the Origin and
Early Evolution of Birds*

A new perspective on the origin of endothermy

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ABSTRACT

A new hypothesis for the origin of endothermy in birds is discussed. I suggest extensive parental care provided the initial impetus for the evolution of endothermy. Among extant animals one of the most important functions of an endothermic metabolism is the incubation of embryos. Furthermore, I propose that extensive parental care is a key innovation that greatly influenced much of the homoplasy observed in extant birds and mammals, including their extraordinary ability to sustain vigorous exercise and their parasagittal postures.

KEYWORDS

Parental care, endothermy, thermogenesis, reproduction, hormone, aerobic capacity.

Introduction

The recent discoveries of flightless but feathered dinosaurs suggest that feathers initially served as insulation, adding to a growing body of evidence that implies dinosaurs, or at least some dinosaurs, were endotherms (Hou 1994; Chen et al. 1998; Ji et al. 1998; Padian 1998). Counterarguments to the ideas that these animals were endotherms and that avian ancestry nests within Theropoda have been proposed based on the purported activity metabolism and lung structure of theropods (Ruben et al. 1997). However, close examination of the alleged causal linkage between endothermy and a great capacity for vigorous aerobic activity indicates that the physiological foundation for these arguments is not well founded. Because the ability to sustain vigorous exercise mandates specialization of many anatomical and physiological features involved in the oxygen cascade (see Table 1), it has been widely assumed that these features entail some sort of maintenance cost that increases basal (standard) metabolic rates (Regal 1975; Heinrich 1977; Bennett and Ruben 1979; Pough 1980) (see the Appendix for definitions of selected terminology used throughout this paper). Yet a physiological basis for this purported maintenance cost has not been identified (Bennett and Ruben 1979; Bennett 1991; Hayes and Garland 1995). Hence, although endotherms generally can sustain vigorous exercise better than ectotherms, a cause and effect relationship has never been established.

Endothermy may not have arisen so that animals could sustain exercise; instead, an endothermic metabolism may have resulted in selection for greater aerobic capacity. Because endotherms need significantly more food than ectotherms (Bennett and Nagy 1977), and because active foragers obtain more food than sit-and-wait predators (Anderson and Karasov 1981), an active foraging strategy is well suited to endothermy (Bakker 1980). Active foraging mandates an ability to sustain vigorous exercise (Taigen et al. 1982). Thus, the elevated food requirements of endothermy may have mandated a greater ability to sustain vigorous exercise. Hence, previous ideas linking activity metabolism and endothermy may have confused the rea-

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TABLE 1. Homoplasious avian and mammalian characters.

	Thermoregulation	Reproduction	Endurance	Communication
<i>Plesiomorphic characters for amniotes</i>	Controlled by the hypothalamo–hypophysial axis of the brain	Controlled by the hypothalamo–hypophysial axis of the brain	Controlled primarily by the medulla and pons centers of the brain, and autoregulation	Rudimentary hearing
	Thyroid hormones increase thermogenesis and other roles in integument	Thyroid hormones cause gonadal maturation and other roles in embryo growth and development		No vocalization in most groups
<i>Characters independently evolved in birds and mammals</i>	Insulation (e.g., hair, feathers, subcutaneous fat)	Extensive parental care; large investment in few offspring	High rates of minute ventilation	Keen hearing
	Significant internal heat production	Embryo incubation	Large pulmonary diffusion capacity	Vocal communication
	Respiratory turbinates	Parental feeding of offspring	High systemic blood pressures	
		Rapid growth rates to sexual maturity	High oxygen carrying capacity of the blood	
		Determinant growth	Large cardiac outputs	
		Formation of milk (crop, mammary glands)	Complete septum in the ventricle	
		Huddling for thermoregulation	Extensive coronary circulation	
		Elaborate nest building	One aorta	
		Pouches for carrying young (e.g., monotreme, marsupials, hatchling pouch of sungrebes, pouch of penguins)	Large tissue diffusion capacity; dense capillary network in skeletal muscle, abundant mitochondria	
		Social systems (e.g., monogamy, colonial nesting, etc.)	A parasagittal posture; gracile limbs	

sons for the correlation of these characters, as well as the polarity of the characters. In addition to endothermy, selection for high speed endurance appears to be tied to many ecological, behavioral and morphological factors (Taigen et al. 1982; Taigen and Pough 1983). For example, factors such as mode of locomotion, food source and distribution, and intraspecific competition for mates may influence selection for aerobic capacity (Taigen et al. 1982; Taigen and Pough 1983). This complex intertwining of multiple factors has resulted, among both extant endotherms and ectotherms, in a broad range of abilities for sustaining vigorous exercise, precluding an accurate assessment of thermoregulatory status based on activity metabolism (Hicks and Farmer 1998, 1999).

Although the major differences between endotherms and ectotherms primarily have been considered to be their mechanisms of thermoregulation and their responses to exercise (Pough 1980), this view overlooks what is perhaps a more profound difference between these groups, their reproductive biology. Almost without exception endotherms have prolonged and extensive parental care, in contrast to ectotherms, which generally make no, or little, parental investment after parturition or oviposition. Because parental care encompasses a wide range of behaviors, morphology and physiology, it may be a key innovation that has greatly influenced the evolution of several characters: endothermy, the ability to sustain vigorous exercise, a parasagittal posture, rapid growth rates, keen hearing and vocal communication, and complex social systems (Farmer 2000). These characters evolved independently in birds and mammals (Gauthier et al. 1988). Hence, parental care may have set convergent evolutionary trajectories in the lineages that gave rise to birds and mammals.

The idea that extensive parental care provided the initial impetus for the evolution of endothermy has some support from the fossil record. Several oviraptorid and troodontid fossils and nests provide evidence of extensive parental care in some dinosaurs (Norell et al. 1994; Dong and Currie 1996; Webster 1996; Varricchio et al. 1997; Clark et al. 1999; Varricchio et al. 1999). Furthermore, these fossils suggest that some coelurosaurian dinosaurs used their body heat to incubate eggs in open nests, just as most birds do today. To find evidence of body insulation, parental care, and perhaps egg incubation in closely related dinosaurs is consistent with the idea that reproduction and basal metabolic rates have coevolved (Sage 1973; McNab 1980, 1987; Thompson and Nicoll 1986; Nicoll and Thompson 1987; Farmer 2000).

Endothermy: The Price That Must Be Paid for High Speed Endurance?

The energetic expense of an endothermic metabolism is considerable. For example, the daily energy requirements of a free-ranging western fence lizard were found to be only 3% to 4% those of a comparably-sized bird or mammal (Bennett and Nagy 1977). Hence the evolution of birds and mammals from ectothermic ancestors suggests that endothermy entails a selective advantage that outweighs this energetic expense. Many hypotheses of how endothermy evolved have been put forward over the past 30 or 40 years, some proposing mechanisms, but most attempting to understand the selective advantage of endothermy. Mechanisms proposed to have led to the evolution of endothermy are a parasagittal posture, which was thought to produce heat by tonic muscular activity (Heath 1968), and stimulation of the Na⁺ pump by thyroid hormones (Stevens 1973). Hypotheses for the selective advantage of endothermy mainly centered around the notion that endothermy expanded capabilities for exercise. Either endothermy enabled activity in a cold niche (Crompton et al. 1978; McNab 1978; Block 1991) or endothermy expanded exercise and endurance (Regal 1975; Heinrich 1977; Bennett and Ruben 1979). The foundation of these latter hypotheses was the idea that the ability to sustain vigorous exercise required specialized biochemical, anatomical or physiological features with an accompanying maintenance cost; endothermy was the price that had to be paid for high speed endurance (Regal 1975; Heinrich 1977; Bennett and Ruben 1979; Pough 1980).

Of the hypotheses that relate endothermy to activity metabolism, one of the most widely accepted is the aerobic capacity model (Bennett and Ruben 1979). This model proposed that basal (standard) metabolic rates (BMR) are linked to the maximal rates of oxygen consumption

(VO_{2max}) by an unknown physiological mechanism. Consequently, these characters were constrained to coevolve. As natural selection favored animals with the ability to sustain vigorous exercise (mandating ever larger VO_{2max}), BMR invariably increased. In support of this theory, Bennett and Ruben (1979) stated that the ratio of VO_{2max} to BMR (a quantity known as the aerobic scope) of extant vertebrates is fixed between about 5 and 10. Furthermore, they pointed out that the VO_{2max} of an endotherm is about 10 times greater than that of an ectotherm and that the basal metabolic rate of an endotherm is about 10 times greater than the standard rate of an ectotherm. Hence, as selection acted to increase VO_{2max} , BMR was also elevated, resulting in the evolution of endothermy.

Despite its popularity, there are problems with the aerobic capacity hypothesis. The physiological mechanism purported to link basal and maximal rates of oxygen consumption has never been identified. Indeed, a physiological linkage may not exist. The elevated metabolism associated with endothermy in mammals is largely a product of leaky cell membranes in the visceral organs, while the elevated metabolism of sustained vigorous activity primarily results from energy used by skeletal muscles to produce physical work (Ishmail-Beigi and Edelman 1970; Weibel 1984; Else and Hulbert 1985; Hulbert 1987; Hulbert and Else 1990; Else et al. 1996) (Table 1). Furthermore, if a mechanism links these two characters, then an increase in VO_{2max} should result in a parallel increase in BMR. However, empirical data in humans indicate that exercise conditioning can significantly elevate VO_{2max} without increasing BMR (Bingham et al. 1989; Meredith et al. 1989; Frey-Hewitt et al. 1990; Schulz et al. 1991; Broeder et al. 1992a, 1992b; Horton and Geissler 1994; Bullough et al. 1995; Wilmore et al. 1998). Although a few studies do show a change in BMR with exercise training, this may be due to inadequate assessment of basal rates. When diet, energy flux, excess postexercise oxygen consumption, and relative proportions of lean body mass are taken into account, it does not appear that exercise conditioning affects BMR (Bullough et al. 1995).

Consistent with these data from humans, most studies of other vertebrates have not found the expected correlation between basal and maximal rates of oxygen consumption, both on the intraspecific and interspecific level. For example, data compiled from the literature provided some support for a correlation on the intraspecific level, but the correlations were fairly weak (Hayes and Garland 1995). However, unlike most studies on humans, very few comparative studies fully take into account factors such as relative proportions of lean body mass and dietary energy flux. Because these factors can influence measurements of BMR and VO_{2max} , failure to account for these variables can give a false impression that a correlation exists. For example, both a fat and a lean animal could have the same BMR and VO_{2max} with respect to lean body mass, but the heavier individual will have both a lower BMR and VO_{2max} on a total body weight basis, giving the false impression of a correlation. Because of the potential for an artificial bias, a weak correlation on the intraspecific level is troublesome.

On the interspecific level, the correlation between VO_{2max} and BMR is even less significant (Hayes and Garland 1995). Although aerobic scopes were proposed by Bennett and Ruben (1979, 1986), to range between 5 to 10, data indicate that aerobic scopes are far more variable than this. For example, in amphibians they range from between 6 and 26 (Taigen et al. 1982); in reptiles from 5 to 30 (Bennett 1982); in birds from approximately 5 to 36 (Tucker 1968; Bundle et al. 1999); and in mammals (the group that has been best studied) from about 3 to 60 (Morrison et al. 1959; Weibel et al. 1992). This variability does not support the notion that aerobic scopes are fixed. Furthermore, data from two closely related scombroid fishes, tuna and mackerel, suggest that ectothermic mackerel have as great an aerobic capability as endothermic tuna (Freund and Block 1998), which is inconsistent with the aerobic capacity model. Finally, studies of laboratory mice that have been bred for increased VO_{2max} do not show a concomitant increase in BMR (Konarzewski et al. 1997). Hence, the preponderance of the data does not support the hypothesis that VO_{2max} and BMR are constrained to coevolve due to a physiological linkage.

Like the aerobic capacity model, other hypotheses put forward for the evolution of en-

dothermy have merit, as well as counterarguments that have been reviewed elsewhere (Hayes and Garland 1995). Hence, it seems we lack a full understanding of the selective benefits of an endothermic metabolism in birds and mammals. A recently proposed hypothesis suggests that endothermy in these groups is simply one character among many that serve the function of parental care (Farmer 2000).

Extensive Parental Care: A Key Innovation

Among the most fascinating aspects of vertebrate evolution are the many characters that are shared by birds and mammals but that evolved independently (Table 1). Although it has been proposed, based on these similar features, that birds and mammals constitute a monophyletic group (Owen 1866–68; Gardiner 1982; Løvtrup 1985), fossil evidence indicates that these shared features are the result of a remarkable convergent evolution (Gauthier et al. 1988). Birds and mammals arose from basal amniotes and have had separate evolutionary histories since the Carboniferous, roughly 340 my ago (Lombard and Sumida 1992; Sumida 1997). Therefore the homoplasious avian and mammalian phenotypes suggest that there have been similar selective pressures working on these groups for a similar function. One function that could explain the convergent evolution of many of these characters is parental care.

Extensive parental care may be a key innovation that predestined much of the convergent evolution that occurred in the avian and mammalian lineages. A key innovation is used here to denote a change that sets in motion the evolution of other functionally interacting characters (Mayr 1960; Liem 1973; Levinton 1988). Selection for extensive parental care appears to have set in motion the evolution of a suite of functionally related characters, including: (1) an endothermic metabolism, which enables a parent to control incubation temperature; (2) an aerobic activity metabolism and a parasagittal posture, which enable parents to forage widely for themselves as well as for their offspring; (3) keen hearing and vocalization, which facilitate parent–offspring communication; and (4) complex social systems, which can enhance the care of offspring. The evolution of endothermy, a parasagittal posture, and an aerobic activity metabolism have received considerable attention with regards to the evolution of dinosaurs (Bakker 1971; Bennett and Dalzell 1973; Ostrom 1980; Farlow 1990). Here, these characters are re-examined with respect to their importance and function in parental care in extant animals. I propose that parental care is a common focus for selection that can account for the convergent evolution of these characters in the avian and mammalian lineage. I support this hypothesis with examples of functional convergence in a wide range of organisms.

Parental incubation of embryos: a selective advantage of endothermy

The ability to control temperature during reproduction has evolved independently an extraordinary number of times, suggesting very strong selection for this trait. For example, multiple lineages of insects have evolved the capability of controlling temperature during embryonic development. Characters that confer this ability, some of which are highlighted below, include many structures and behaviors that are also found in amniotes and serve the same function. The presence of similar structures and behaviors in amniotes and insects that serve the function of embryo incubation suggests that a similar selective regime has given rise to their evolution.

INSULATION. In extant mammals and birds, the presence of insulation (such as hair, feathers and subcutaneous fat) is an important adaptation that enables body temperature to be elevated above ambient temperature. Similarly, the presence of insulation in insects can be instrumental in increasing body temperature. For example, the hair-like setae of gypsy moth caterpillars act as insulation that enables elevated body temperature during the late instar stage of the life cycle (Casey and Hegel 1981). Many moths and bumblebees are insulated with hair (pile) and scales (Heinrich 1974, 1979).

Many birds, mammals, lizards, snakes and crocodylians build nests during reproduction that provide insulation and facilitate control over developmental temperatures (Shine 1988).

Similarly, by constructing nests insects provide an environment for developing offspring that is warm and equable. Ants, termites, wasps, honeybees and bumblebees have all independently acquired the ability to construct elaborate nests in which nursery chambers are warmed by the metabolic heat of the adults (Wood 1971; Heinrich 1979; Seeley and Heinrich 1981; Hölldobler and Wilson 1994). Although incapable of constructing nests themselves, caterpillars of the wax moth live in the abandoned hives of bees and use metabolic heat to raise developmental temperatures (Heinrich 1981).

HUDDLING. Both insects and amniotes huddle during reproduction to effectively increase body mass for thermoregulatory reasons. Because insects are small they have a high surface area to volume ratio and generally maintain body temperatures that are negligibly different from ambient. However, by huddling together a group of insects can use their metabolic heat to elevate developmental temperatures. For example, army ants form bivouacs with their own bodies, with the queen and eggs placed in the center of the swarm to be warmed by the metabolic heat of the group (Hölldobler and Wilson 1994). Furthermore, aggregation is often used in conjunction with a nest to control developmental temperatures. For example, ants, termites, bees and wax moth caterpillars aggregate or disband to keep nests at a warm and stable temperature (Wood 1971; Heinrich 1979, 1981; Hölldobler and Wilson 1994). Similarly, in many vertebrates (such as emperor penguins and mice), aggregation during reproduction has a thermoregulatory function (Jouventin 1975; Hill 1992).

SOLAR BASKING. In some lizards, snakes and ants, adults bask in the sun and then return to the nest to transfer the heat from their bodies to embryos (for example, *Eumeces fasciatus*, *Elaphe obsoleta*, *Python regius* and *Morelia spilotes*) (Shine 1988; Hölldobler and Wilson 1990). Furthermore, some ants and lizards regulate developmental temperature by transferring their eggs to different depths in a nest (*Eumeces fasciatus* and *Ophisaurus ventralis*) (Shine 1988; Hölldobler and Wilson 1990). Manipulation of embryo location for the purpose of thermoregulation is thought to be one of the dominant selective factors in the evolution of viviparity (retainment of embryos internally) (Guillette et al. 1980; Guillette 1982; Shine 1985, 1987, 1989). There is apparently very strong selection for this trait in amniotes, as it has been acquired independently approximately 100 times within squamate reptiles (Shine 1991).

INCUBATION THROUGH THERMOGENESIS. Most significantly, thermogenesis is important during reproduction in a broad range of organisms. For example, some plants of the family Araceae have metabolic rates during reproduction that are comparable to those of flying hummingbirds (Nagy et al. 1972). This heat serves to volatilize scents that attract pollinators. High rates of oxygen consumption are also found during reproduction in the flagellate protozoan *Euglena gracilis*. Most of this oxygen is used to produce heat to speed up reproduction, rather than yielding chemical energy (Heinrich and Cook 1967). In a wide variety of animals, thermogenesis is used to elevate incubation temperatures above ambient. For example, among amniotes not only birds and mammals use metabolic heat for embryo incubation, but pythons also incubate their young (Van Mierop and Barnard 1978). With the help of insulation provided by an incubation mound, brooding female pythons maintain a body temperature differential above ambient of 9°C to 13°C (Shine 1988). Some crocodylians and some megapode birds keep their eggs warm with the heat produced by bacteria during the decomposition of organic matter (Lang 1987; Jones et al. 1995). Among insects, vespine wasps and the European hornet (*Vespa crabro*) use metabolic heat generated by muscular contractions to incubate their broods (Ishay and Ruttner 1971; Heinrich 1979; Seeley and Heinrich 1981). Furthermore, in both honeybees and bumblebees a large portion of the energy profit from foraging is used to regulate nest temperature to provide a suitable environment for the development of their young (Heinrich 1979). When incubating, adult bumblebees position their abdomens next to the young; heat generated through contraction of thoracic musculature is transferred to the

ventral abdomen by a specialized circulatory system. Although the bee is covered by a hairlike layer of insulation, a region of the abdomen is bare so that heat can be transferred from the body to the young through this thermal window (Heinrich 1979). This morphology is remarkably similar to the brood patch in birds, which consists of a region of the breast or abdomen that is bare of insulation and contains a specialized circulatory system to direct heat from the body of the adult to the eggs.

Many examples of convergent structures and behaviors that function for embryo incubation are found among insects and amniotes. Huddling, the construction of elaborate nests, basking and returning to offspring to transfer heat from the body of the adult to offspring, manipulation of egg position, the presence of incubation patches, and incubation through thermogenesis are all examples of homoplasious characters that function in embryo incubation.

THE SELECTIVE ADVANTAGES OF EMBRYO INCUBATION. Developmental processes are very sensitive to temperature. Developmental temperature affects: (1) the viability of embryos; (2) the presence or absence of developmental defects; (3) the length of the incubation period; and (4) the expression of phenotypic plasticity that may play an integral role in many life history phenomena (e.g., behavior, growth rates, basal metabolic rates, antipredator tactics, and so on).

Generally a temperature range that is easily tolerated by an adult is lethal to an embryo (Packard and Packard 1988). For example, most avian embryos will die if exposed for several hours to temperatures that fall outside the range of 36°C to 39°C (Webb 1987). Similarly, crocodylian eggs will not hatch normally if incubated outside the range of 28°C to 34°C (Ferguson 1985). Development will not take place in the lizard *Iguana iguana* if temperatures deviate by more than 2°C from the optimum of 30°C (Licht and Moberly 1965).

Incubation at the extremes of the viable range can produce developmental defects. In fish the number of fin rays (dorsal, anal and pectoral) is determined by the developmental temperature of the larvae (Taning 1952). In reptiles deformations of the limbs, central nervous system and eyes, loss of the lower jaw, facial clefting, abnormal formation of the vertebral column, increased numbers of the vertebrae in the trunk, and ventral hernias result from developmental temperatures that deviate too greatly from the optimum (Yntema 1960; Webb 1977; Muth 1980; Webb et al. 1983; Ferguson 1985; Burger et al. 1987; Deeming and Ferguson 1991). Similar abnormalities are found in birds when developmental temperatures deviate from the optimum (Romanoff 1972).

Because temperature critically affects the rates of cellular processes, it can have a dramatic impact on developmental periods. For example, in the lizard *Dipsosaurus dorsalis* an increase in developmental temperature from 28°C to 32°C shortens the incubation period by 27 days (from about 85 to 58 days), and an increase from 28°C to 38°C shortens the period by about 40 days (from about 85 to 45 days) (Muth 1980). Incubation periods can affect the risk of predation and disease. They are also important for adjusting hatching with seasonal food supplies.

However, one of the most important effects that incubation temperature can have in amniotes is to induce the expression of phenotypic plasticity. Mothers may be able to actuate particular developmental pathways by controlling incubation temperature (Qualls and Shine 1996; Shine and Harlow 1996; Shine et al. 1997; Shine 1999). For example, maternal care in water pythons includes thermogenesis for embryo incubation. In this species, different embryological thermal regimes influence offspring morphology (size and shape), locomotor performance (swimming ability), behavior (escape tactics, propensity to strike, willingness to feed in captivity), and growth rates (Shine et al. 1997). Incubation temperature has been observed to effect many characters in other vertebrates as well, such as post-hatching growth rates, molting cycles, pigmentation patterns, scalation, thermal preferences, running speed and (in some species) the sex of individuals (Fox 1948; Osgood 1978; Packard and Packard 1988; Deeming and Ferguson 1991; Norris 1996; O'Steen 1998; Shine 1999). Thus a potential selective advantage of thermogenesis is that it enables parental manipulation of offspring phenotypes. This ability could play an integral role in adaptive modification of life history phenomena (Shine 1995).

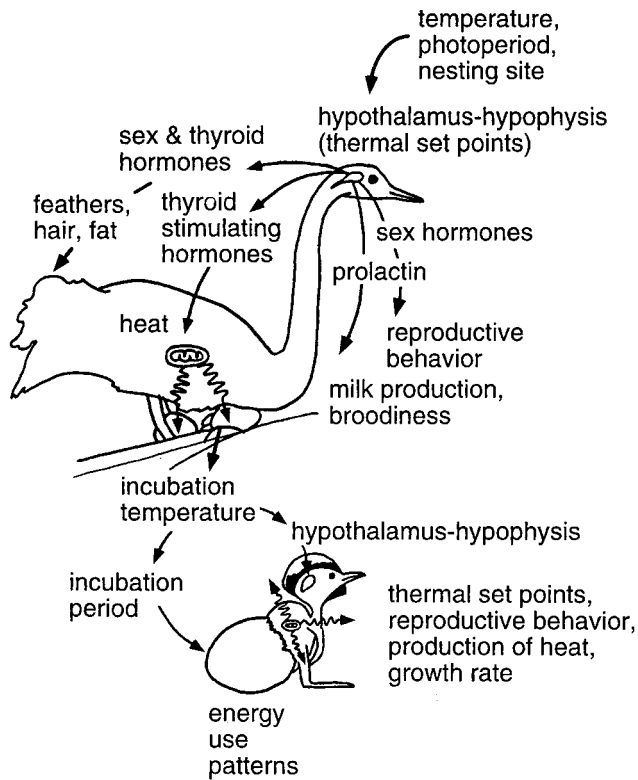


FIGURE 1. The early evolutionary steps to endothermy in archosaurs may have entailed manipulation of incubation temperature through thermogenesis. Maternal manipulation of incubation temperature can influence the phenotype of offspring and thus affect the reproductive biology of the next generation. Incubation temperature during embryogenesis can significantly influence many developmental trajectories. In reptiles, characters that have been found to be altered by incubation temperature include: locomotor abilities; growth rates; basal (standard) metabolic rates; integumentary features (shedding, scalation and coloration); and behavior (see text for references). These effects are probably largely mediated through a “setting” of the embryological hypothalamus. In a reproductive adult various external stimuli (such as photoperiod, ambient temperature, and others) operate through the hypothalamus–hypophysis axis of the brain to cause the release of hormones. These hormones can both increase metabolic rates (and therefore thermogenesis) and affect reproductive behavior and physiology.

The expression of phenotypic plasticity by incubation temperature is probably largely mediated through a region of the brain known as the hypothalamus (Deeming and Ferguson 1991). It has been suggested that incubation temperatures permanently alter the development of the embryological hypothalamus and that therefore these temperatures have feedback effects throughout the life of the hatchling by various pathways: basal metabolic rate and thermal set points are altered by thyroid hormones, growth is altered by growth hormones, skin properties are altered by the sex and thyroid hormones, and behavior (especially reproductive behavior) is altered by the sex hormones (Deeming and Ferguson 1991).

The hypothalamo–hypophysial axis of the brain has several important functions. First, it is the center of the brain that acts as a thermostat, sensing the temperature of the body and initiating mechanisms to increase or decrease body temperature (such as sweating, panting, shivering or alteration of basal metabolic rates). Second, it is the area of the brain that regulates the secretion of hormones that play important roles in reproduction, behavior and basal metabolism. In a reproductive adult environmental stimuli such as photoperiod, temperature and the suitability of mates and nest sites operate through the hypothalamo–hypophysial axis to initiate

and control reproduction (Deeming and Ferguson 1991). The secretion of various hormones influences courtship, breeding, parental behavior and thermoregulatory behaviors.

Hence, the "decision" of a mother to incubate her young, and her ability to produce heat to accomplish this incubation, could affect the phenotype of her offspring in such a way as to concomitantly alter anatomical, physiological and behavioral traits conducive to an endothermic thermoregulatory strategy: the "decisions" of the offspring to provide parental care; their thermogenic abilities (basal or standard metabolic rates); integumentary properties that potentially could provide insulation (the buildup and shedding of scales); growth rates to sexual maturity; and locomotor capabilities, among others. (see Figure 1, Table 1). Unlike other hypotheses for the evolution of endothermy, the parental care hypothesis offers an explanation for a simultaneous change in a suite of characters associated with endothermy.

A MECHANISM LINKING THERMOGENESIS TO REPRODUCTION. With the parental care hypothesis for the evolution of endothermy, a plausible mechanism exists that could account for the evolution of nonshivering thermogenesis. The initial thermogenesis of endothermy may have involved the elevation of basal (standard) metabolism (and therefore thermogenesis) resulting from the secretion of thyroid and other hormones during the reproductive period. As previously noted, both basal (standard) metabolic rates and reproduction are controlled by the same axis of the brain through the secretion of hormones (Figure 1, Table 1). Many of these hormones have dual roles in both of these processes. Thyroid hormones are particularly noteworthy in this regard. Early in vertebrate evolution thyroid hormones appear to have been important primarily for gonadal maturation, and it is important to note that thyroid cycles are positively correlated with reproductive cycles in most vertebrates (Sage 1973). Although they have retained this reproductive role in amniotes, thyroid hormones are also involved in the control of basal metabolic rates, thermogenesis, growth, and properties of the integument (Norris 1996). Because the levels of thyroid and other thermogenic hormones are elevated during reproduction, it is not surprising to find that metabolism is elevated during reproductive periods. For example, during reproduction metabolic rates (and thus thermogenic abilities) have been found to be elevated over nonreproductive levels in humans, tenrecs, short-tailed opossums, elephant shrews, snakes and lizards (Clausen 1936; Van Mierop and Barnard 1978; Guillette 1982; Birchard et al. 1983; Thompson and Nicoll 1986; Prentice and Whitehead 1987; Forsum et al. 1988; Beuchat and Vleck 1990; Butte et al. 1999).

However, not only do thermogenic abilities change during reproduction, but body temperature set points also can be altered. For example, nonreproductive pythons are ectothermic; that is, they lack a high rate of internal heat production and their body temperatures track the ambient. However, a gravid or brooding snake is endothermic; when ambient temperature drops the animal shivers to produce heat and maintain a warm body temperature (Van Mierop and Barnard 1978; Slip and Shine 1988; Shine et al. 1997). Pythons are not alone in exhibiting a pronounced change in body temperature set points and thermoregulatory behavior during reproduction. Many viviparous lizards and snakes alter their thermoregulatory behavior to decrease body temperature fluctuations compared to nonreproductive females (Charland and Gregory 1990; Charland 1995). Furthermore, mean body temperature set points often change (Beuchat 1986; Charland 1995).

Similar changes are found in other amniotes. Many heterothermic mammals and birds, whose body temperatures can be largely dependent on the ambient temperature, increase their thermogenic capabilities and alter body temperature set points during pregnancy or while brooding. For example, tenrecs become better endotherms when pregnant; that is, basal metabolic rates increase, mean body temperature increases and, in the face of varying environmental temperatures, body temperature fluctuations decrease (Nicoll and Thompson 1987; Stephenson and Racey 1993; Poppit et al. 1994). Like tenrecs, sloths are considered to have a low potential for heat production and inferior ability to thermoregulate compared to many other mammals. However, pregnancy enhances thermoregulatory and thermogenic abilities (Dawson

1973 and references therein). Similarly, pregnancy changes thermoregulation in bats. Pregnant females maintain a higher mean body temperature and reduce the time spent in torpor compared to nonpregnant bats (Audet and Fenton 1988; Hamilton and Barclay 1994). Torpor is also less likely in pregnant than nonpregnant hedgehogs (Fowler 1988). Hummingbirds generally become torpid at night to save energy (Huxley et al. 1939; Bartholomew et al. 1957; Calder 1971); in contrast, when incubating eggs females generally maintain homeothermic endothermy (Howell and Dawson 1954; Calder 1971; Calder and Booser 1973). For example, the Calliope hummingbird, the smallest bird in temperate North America, incubates her eggs even when night temperatures dip to near freezing (0.2°C) (Calder 1971). Although dormant and hibernating, pregnant bears maintain warm body temperatures (Watts and Hansen 1987). Thus it appears that high metabolic rates and warm body temperatures are either advantageous or essential during reproduction in mammals and birds (Thompson and Nicoll 1986; Nicoll and Thompson 1987). Because the same axis of the brain controls both reproduction and basal metabolic rates, it is not surprising that reproduction and basal metabolism appear to have co-evolved (Sage 1973; Thompson and Nicoll 1986; Nicoll and Thompson 1987; Farmer 2000).

In summary, a selective advantage of a high metabolic rate in birds, mammals and pythons seems to be that it gives parents the ability to incubate their embryos. This idea is supported by the following observations: (1) the importance of incubation temperature to the viability of offspring, to their proper development, to the length of the incubation period, and to the expression of phenotypic plasticity; (2) the many examples where metabolic heat functions to incubate young in diverse groups of animals; (3) the common regulatory system of basal (standard) metabolic rates and reproduction (the hypothalamo–hypophysial axis of the brain); and (4) the fact that during reproductive periods metabolic rates can increase and body temperature set points are altered.

Thus endothermy may be a facet of parental care. Extensive parental care may be a key innovation that explains the presence of characters besides endothermy found in both birds and mammals. Many of these characters, such as a parasagittal posture and an expanded aerobic activity metabolism, have previously been directly linked to the evolution of endothermy (Heath 1968; Bakker 1971; Regal 1975; Heinrich 1977; Bennett and Ruben 1979; Ostrom 1980). However, the “correlation” of these characters may not indicate causation but selection for a common, convergent reproductive strategy.

High speed endurance to feed offspring

A major aspect of parental care in all mammals and most birds is the provisioning of food to young. This contrasts with ectotherms, which rarely provide food to offspring. There are several advantages to feeding young. First, an adult can make use of food sources unavailable to juveniles that cannot digest them or lack the strength and skill to obtain them. Second, provisioning of food to young enables more rapid growth (Pond 1977; Ricklefs 1979). Rapid growth may be especially important in environments where predation rates among juveniles are high (Williams 1966).

Although there are clearly advantages to parental feeding of young, this requires a parent to obtain more food. The size of this extra burden varies, depending on such things as food source and distribution, the number of offspring and how precocial or altricial they are, the cost of foraging, whether one or both parents share the burden, and whether or not there are other contributors (such as older siblings from previous clutches or other members of a social unit). However, in spite of the complex intertwining of multiple factors, the bottom line is that the energy cost of feeding young is often very great. For example, during peak lactation the mean daily energy requirements are several times greater than for nonreproductive adults (from 400% to over 1000% of basal metabolic rates) (Clutton-Brock 1991; Thompson 1992). Similarly, avian parents generally need to obtain from three to five times more energy than nonreproductive adults (Walsberg 1983). This increased energy requirement escalates foraging efforts (Walsberg 1983; Lee and Cockburn 1985; Rydell 1993), sometimes to an astonishing level. For example,

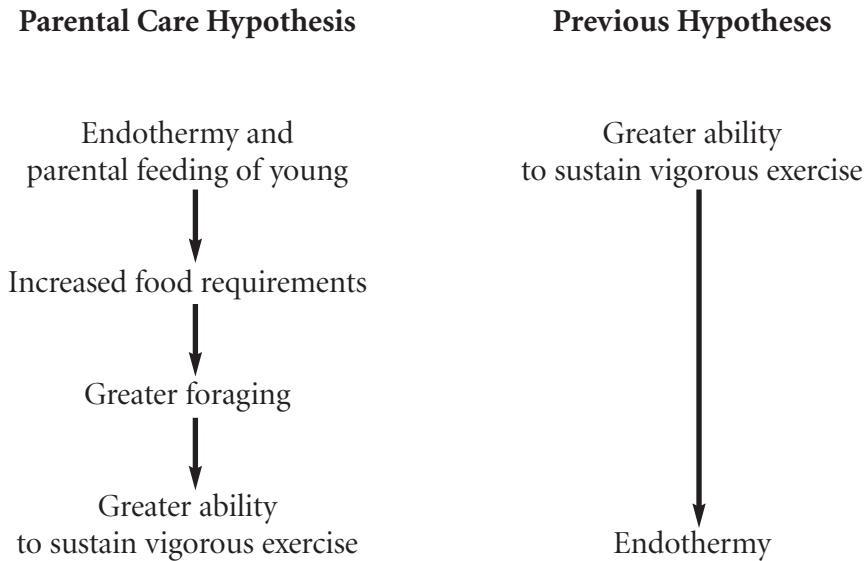


FIGURE 2. The polarity of endothermy and the ability to sustain vigorous exercise. In the parental care hypothesis for the evolution of endothermy it is proposed that both endothermy and provisioning offspring with food increase daily energy requirements and, therefore, increase selection for an active foraging mode and the ability to sustain vigorous exercise. This contrasts with previous hypotheses for the evolution of endothermy, which propose that selection for greater abilities to sustain vigorous exercise resulted in the evolution of endothermy (Regal 1975; Heinrich 1977; Bennett and Ruben 1979; Pough 1980).

when gathering food for young the common swift of Europe will fly 1000 km a day. The European pied flycatcher will make approximately 6200 foraging trips to raise a brood (Gill 1995).

I propose that these elevated foraging requirements have influenced the evolution of exercise metabolism in the lineages that gave rise to birds and mammals. Foraging over long distances or for long periods of time must be powered by the aerobic production of ATP. To synthesize ATP rapidly through aerobic pathways, oxygen must be brought into the lungs with ventilation, must diffuse into the blood and be transported by the heart to the muscle, where it diffuses to the site of ATP synthesis, the mitochondria. This process is known as the oxygen cascade. Birds and mammals have evolved in parallel remarkably similar features of the oxygen cascade (Table 1; Farmer 1999, 2000). As previously mentioned, it has long been thought that the evolution of these features and the ability to sustain vigorous exercise entailed a maintenance cost that led to the evolution of endothermy (Regal 1975; Heinrich 1977; Bennett and Ruben 1979; Pough 1980). In contrast, I propose that the evolution of thermogenesis and parental feeding of young escalated food requirements and therefore intensified selection for an aerobic exercise metabolism (Figure 2). The evolution of a highly aerobic activity metabolism certainly involved many changes in the organ systems of the oxygen cascade (Table 1; Farmer 1999). However, these organ systems do not work in isolation but are affected by the body in which they are housed. Postural and ventilatory innovations may have been prerequisite to the evolution of high rates of respiratory gas exchange.

The correlation of posture and metabolism

The functional significance of a correlation between posture and metabolism has engendered much controversy; generally, extant endotherms have a parasagittal posture while extant ectotherms have retained a sprawling posture. The parasagittal posture of most dinosaurs has therefore been suggested to be evidence for endothermy in dinosaurs (Bakker 1971). This idea has been criticized on the grounds that no mechanism was identified to link posture to metab-

olism (Bennett and Dalzell 1973). The mechanism previously proposed by Heath (1968), that a parasagittal posture produced heat by tonic muscular mechanisms, was not supported by subsequent research (Bakker 1972; Bennett and Ruben 1986). Although posture cannot be linked to basal metabolic rates directly, a parasagittal posture is probably related to activity metabolism and foraging mode (Bakker 1980). An adequate means of pumping air into and out of the lungs is a prerequisite for high rates of oxygen consumption. The sprawling posture that is ancestral for tetrapods appears to have constrained simultaneous costal ventilation and rapid locomotion (Carrier 1987a, 1987b). Innovations found in archosaurs and mammals, such as the diaphragm of mammals and crocodylians and a parasagittal posture, were proposed to have facilitated simultaneous running and costal ventilation and to have enabled these lineages to increase their aerobic exercise metabolisms. The idea that ventilation has been a bottleneck for rapid exchange of respiratory gases due to a mechanical constraint on simultaneous running and costal ventilation has recently received additional support (Hicks and Farmer 1998, 1999; Owerkowicz et al. 1999). However, this constraint is related to aerobic activity metabolism and is not directly related to basal metabolic rates.

In summary, although in general endotherms have a greater ability to sustain vigorous exercise than ectotherms, and endotherms tend to have a parasagittal posture while ectotherms retain a sprawling posture, these characters appear to be broadly correlated because of foraging strategy and food requirements (Bakker 1980; Taigen et al. 1982; Taigen and Pough 1983; Carrier 1987a) and hence have probably been greatly influenced by the reproductive strategy of parental feeding of young. Furthermore, as previously mentioned, other factors may increase the variability of these correlations (such as intraspecific competition for mates, modes of locomotion, food source and distributions, and so on) (Taigen et al. 1982; Taigen and Pough 1983). Ideas suggesting these characters are linked by a physiological mechanism—in other words, that a parasagittal posture produces heat by tonic muscular mechanisms or that an unidentified physiological mechanism links endothermy and an aerobic exercise metabolism (Heath 1968; Bennett and Ruben 1979; Ruben et al. 1997)—have not been supported by subsequent neontological studies. Consequently, great caution is called for when relying on fossil indicators of activity metabolism (such as posture, gracile limbs, and mechanisms of ventilation) to deduce the thermoregulatory status of extinct animals.

The Evolution of Parental Care

Endocrinologists and other biologists interested in reproduction have long suggested that basal metabolic rates and reproduction have evolved hand in hand (Sage 1973; McNab 1980; Nicoll and Thompson 1987; Thompson 1992; Norris 1996). In previous papers that discussed the evolution of endothermy and the reproductive biology of mammals and dinosaurs, endothermy was proposed to be a nonreproductive factor that profoundly affected reproduction in these lineages (Hopson 1973; Guillette and Hotton 1986; Coombs 1990). In contrast I propose that the evolution of extensive parental care not only preceded the evolution of endothermy, but provided the initial impetus for the evolution of this trait. Unfortunately, the polarity of these characters is somewhat ambiguous. However, there is no reason to assume a priori that endothermy preceded the evolution of parental care; indeed, there is some precedence to suggest the opposite polarity.

Assessing the origin of nonfossilized characters, such as parental care, in extinct taxa is sometimes possible by mapping onto a phylogeny the presence of the character in extant animals that bracket the extinct taxa of interest. In my opinion, this approach does not yield a clear result with respect to the evolution of parental care (Figure 3). Among Sarcopterygii, parental care is found in the form of viviparity in the coelacanth (Millot et al. 1978; Wake 1985), in two of the three genera of lungfish (*Lepidosiren* and *Protopterus*) (Carter and Beadle 1931; Greenwood 1987), in many amphibians (Shine 1988; Guillette 1989; Clutton-Brock 1991), in all mammals (Clutton-Brock 1991), in many lepidosaurs (Shine 1988), in all crocodylians (Shine 1988), and in almost all birds (Clutton-Brock 1991; Jones et al. 1995). Although present in many

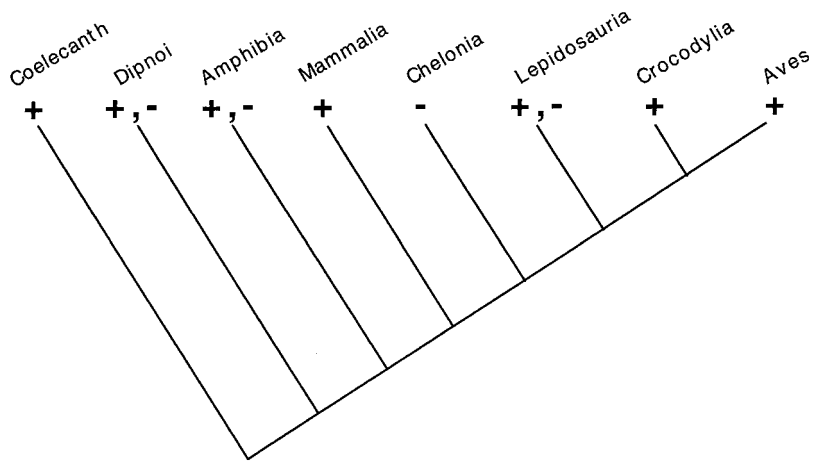


FIGURE 3. Hypothesized relationships of Sarcopterygii illustrating the presence (+) or absence (-) of parental care (see text for references).

groups it may be independently derived in most. For example, it has been suggested that parental care among nonavian diapsids evolved independently more than 120 times (Shine 1988, 1989). Although a parsimonious view of the evolution of parental care in archosaurs is that it was present before crocodylians and birds diverged (Varricchio et al. 1999), the many times that parental care has evolved throughout the animal kingdom lends little confidence to parsimony.

However, several animals show that endothermic neonates do not mandate parental care and that parental care probably preceded or at the least coevolved with the evolution of endothermy. The neonates of megapode birds receive no parental care, but parental care of the eggs is present in most species and involves control of incubation temperature (Jones et al. 1995). Furthermore, the only known facultative endotherms are pythons. Parental care has evolved independently many times in snakes (Shine 1988); there is no precedence for assuming that facultative endothermy preceded and resulted in parental care in pythons. Hence, it seems probable that parental care in the form of egg protection or behavioral control of developmental temperatures preceded the evolution of embryo incubation by thermogenesis.

Conclusion

The discoveries of feathered dinosaurs have not only reinforced the idea that avian origins nest within theropod dinosaurs, but have also provided new and compelling evidence that nonflying theropod dinosaurs were endotherms. Although a great deal of thought has been given to the origin of endothermy in birds and mammals, questions remain as to the selective advantages of this thermoregulatory strategy and the mechanisms that enabled elevated basal metabolic rates. Here, a recently proposed scenario for the evolution of endothermy in birds and mammals was reviewed and contrasted with several previous theories. I have suggested that the initial selective advantage of endothermy was that it enabled an animal to provide offspring with a warm and equable thermal environment during development. Thus endothermy has functioned in parental care. The parental care hypothesis for the evolution of endothermy is distinct from all previous hypotheses in three ways. First, it provides a selective advantage for the evolution of endothermy (embryo incubation) as well as suggesting a mechanism for the thermogenesis (elevation in metabolic rates during the reproductive period due to the secretion of hormones). Second, the parental care hypothesis proposes that endothermy did not initially provide a survival advantage to an individual organism, but benefited the offspring of that individual by providing a favorable environment for development. Third, and most importantly, this hypothesis connects the evolution of endothermy to a common, convergent reproductive strategy. Because

parental care encompasses a wide range of behaviors, morphology and physiology, it may be a key innovation that can account for most convergent avian and mammalian characters.

These characters include an extraordinary ability to sustain vigorous activity and a parasagittal posture. Both endothermy and parental feeding of young increase daily food requirements. Animals with a high food requirement tend to be active foragers. Because sustained active foraging requires the aerobic synthesis of ATP, these animals also tend to have high rates of maximal oxygen consumption. High rates of oxygen consumption mandate high rates of minute ventilation, which, in turn, seems to have required postural and ventilatory innovations. Hence, the reproductive strategy of extensive parental care is central to the biology of both birds and mammals and should not be overlooked when considering the evolution of functionally related characters.

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Appendix: Terminology

Aerobic scope: The ratio of the maximal rate of oxygen consumption divided by the basal metabolic rate (VO_{2max}/BMR).

ATP: Adenosine triphosphate, an important energy compound in cellular metabolism.

BMR: Basal metabolic rate. Refers to measurements made of metabolism under standard conditions such that the effects of thermal stress, digestion metabolism (specific dynamic action or postprandial metabolism), and activity metabolism have been minimized. Although some authors reserve the term “basal metabolism” for use with endotherms and “standard metabolism” for use with ectotherms, others use them interchangeably, a practice that is continued here for the sake of simplicity. Furthermore, measurements made on reproductive animals under the same conditions as basal metabolic measurements are commonly referred to as “resting metabolism” by some authors and as “basal” or “standard metabolism” by others. To emphasize that the only parameter changed is the reproductive state, I have chosen to use basal metabolism for these measurements.

Ectothermy: The thermoregulatory strategy where animals produce very little internal heat and therefore body temperatures track the ambient temperature. External heat sources and sinks are used for thermoregulation.

Embryogenesis: The formation and development of an embryo from an egg.

Endothermy: The thermoregulatory strategy where animals produce significant internal heat so that warm body temperatures can be maintained in the face of a cool environmental temperature.

Heterothermy: Used here to denote endotherms that allow their body temperature to drop with the ambient temperature under some circumstances (as with torpor and hibernation).

Key innovation: A change that sets in motion the evolution of other functionally interacting characters.

Oviparity: The condition of producing young by laying eggs.

Oviposition: The act of laying eggs.

Oxygen cascade: A series of steps in which oxygen moves from the environment to mitochondria. There are four steps in this cascade: (1) bulk movement of oxygen into the lungs with convection by means of ventilation; (2) diffusion of oxygen from the air in the lungs across pulmonary membranes and into the blood; (3) bulk movement of oxygen by the convection of blood from the lungs to capillaries in the tissues; (4) diffusion of oxygen from the blood across the capillary membranes and to the site of ATP synthesis, the mitochondria.

Parasagittal posture: A posture where the elbows and knees are flexed in a parasagittal plane under the hip and shoulder sockets.

Parental care: Any action on the part of the parent made after oviposition that increases the chances of survival of offspring (for example, nest protection, embryo incubation, provisioning of food). Here viviparity is considered a form of parental care (retainment of embryos internally resulting in live birth).

Parturition: The act of delivering live young.

Sprawling posture: A posture where the limbs project out to the sides of the body.

Thermogenesis: The production of heat in the body (as in oxidation).

Viviparity: Retainment of embryos internally to give live birth.

VO_{2max} : The maximum rates of oxygen an animal can consume.